WHY DO EXOTIC TREES INVADE NATIVE VEGETATION IN THE CANTERBURY HIGH COUNTRY?

PETER WARDLE.
Research Associate Landcare Research

At the time of first European occupation, most of Canterbury was clothed in tussock grassland, with smaller areas of swamp, fern and scrub. Pollen from bogs and buried charcoal in the soils, however, show that nearly all this terrain was once forested, and that the forest was burnt some 700 years ago, apparently in the early days of Maori occupation, except where it survived on sheltered lower slopes and in valleys, and in the high rainfall zone in the west. Spread back into the open country has been very slow, largely confined to within a few metres of the margins of remnant stands, and repeatedly set back by further fires.

Since European settlement, native vegetation has been displaced throughout the Canterbury Plains by pasture, crops, shelterbelts, and exotic forests, especially of *Pinus radiata*. Since the advent of aerial topdressing after the Second World War, green pastures have spread across the hills as well, and conifer plantations extend over increasing areas. Through most of this period, however, the 'high country' landscapes remained visually almost unchanged, despite steady infiltration of native vegetation by introduced shrubs and herbs, that in many places now contribute both the majority of species and the largest proportion of the plant cover. Exotic trees have also been spreading, but, for a long time, this spread consisted of isolated trees, established from seed carried by wind or birds, from the sources in plantations, gardens, and shelterbelts. However, such trees have proved to be focal points for further spread; a founder tree is commonly surrounded by numerous offspring. As spread tends to be exponential, its rate may be scarcely noticeable at first, but increases with each generation. Therefore, each year that large stands of wilding pines remain unchecked, the more spectacular the further increase, and the more profound the visual alteration of the landscape.

The exotic trees most frequently escaping into the wild in the Canterbury high country are pines, Douglas fir (*Pseudotsuga menziesii*), larch (*Larix decidua*), and the deciduous broad-leaved trees birch (*Betula pendula*), rowan (*Sorbus aucuparia*), cherry (*Prunus avium*), and sycamore (*Acer pseudoplatanus*). Most of the spread occurs below 1000 m, but *Pinus contorta* in particular establishes vigorously at altitudes far higher than the native beech forest limit which rarely exceeds1400 m in Canterbury.

Where does invasion occur?

Opportunities for invasion are greatly enhanced where the resident vegetation does not completely cover the ground, leaving gaps where immigrant seedlings are not subjected to shading and root competition. Throughout the high country, eroding subsoil, slips, gullies, screes, and recent alluvial deposits are widely available for colonisation by native and introduced plant pioneers, provided there is a seed source within dispersal distance. One might therefore expect native pioneers to predominate, except where there are large concentrations of introduced plants within easy dispersal distance. Yet, it is hard to avoid the impression that in many situations introduced plants, including trees, have inherent and escalating advantages. Braided riverbeds that are pre-empted by willows (*Salix fragilis*) and introduced shrubs long before native trees and shrubs can become established are obvious examples. Experiments in the high country also indicate that various pines and deciduous broadleaved trees and large shrubs can be established more successfully on eroding surfaces than native trees and shrubs. In the vicinity of Craigieburn State Forest, several of these species, including mountain pine (*Pinus mugo*), green alder (*Alnus viridis*), and broadleaf willow (*Salix glaucophylloides*), are now spreading beyond the original plantings.

Invasion is not limited to completely open sites, however. For instance, manuka (*Leptospermum scoparium*) scrub can be invaded by pines, just as it is by native trees. Depleted tussock grassland is also receptive to invasion, in contrast to dense, intact, tall tussock grassland. Douglas fir can spread vigorously into mountain beech (*Nothofagus solandri* var. *cliffortioides)* forest, the most vulnerable stands being those with a fairly open canopy and sparse understorey.

A potential for invasion by exotic trees also exists above the upper limit of native trees. Above the forest limit, there is a grassland belt dominated by snow tussocks, together with areas of scrub. Above this, there is true alpine vegetation of short grassland, cushion-field, and rock- and shingle-dominated surfaces including scree and fell-field. However, experiments are showing that a range of introduced tree species can establish at considerably higher altitudes than the native mountain beech. Some of these are species that grow at alpine tree limits in their countries of origin, e.g. Engelmann spruce (*Picea engelmannii)* from the Rocky Mountains and mountain pine from the European Alps. Even Australian snow gums (*Eucalyptus pauciflora*) can survive 150 m higher than mountain beech. However, currently lodgepole pine (*Pinus contorta*), that scarcely reaches the tree limit in its native North America, is the exotic tree that is spreading most vigorously above the native forest limit.

Are there differences in ecology and physiology between native trees and successful exotic invaders?

Mountain beech and mountain totara (*Podocarpus hallii*) thrive on drier and colder sites than any other large native trees, with mountain beech stands being far more extensive than those of mountain totara and ascending to higher altitudes. Both observation and experiment show that even mountain beech is less well adapted to harsh environments than many exotic species, especially certain pines. The contrast is especially evident at the early establishment stages. Mountain beech seed carries smaller reserves than those of pines, and gives rise to small, delicate seedlings that, lacking deep tap roots and with a relatively low ability to control water loss from their leaves, are more likely to fall victim to drought in open, exposed places. Seedling foliage also seems more inhibited by exposure to full sunlight than those of pines or even snow gum.

Finally, there is a vast difference in frost hardiness, especially in winter, when beech foliage can withstand only down to – 13°C, compared with hardy conifers, which can withstand temperatures far lower than those encountered in our mountains. The cold hardiness of such trees represents adaptation to continental climates with hot summers that enable them to reach far higher altitudes than in oceanic New Zealand, provided they can tolerate the much colder winters. Nevertheless, as noted above, even within

New Zealand some exotic tree species can become established at altitudes well above the upper limit of native trees. The relatively low frost hardiness of mountain beech is probably the feature most responsible for the native 'bush line' not reaching the potential altitudinal limit indicated by these exotics, and also for the treeless 'frost flats' in the valleys. Pines also achieve large dispersal distances, with wildings becoming established at least 10 km downwind from parent trees, compared with circumstantial evidence that beech can disperse to 6 km from parent trees, but only rarely.

Why do native trees seem less well adapted to harsh high country environments than hardy overseas species?

The comparatively low competiveness of our trees in the harsher New Zealand environments is a special case of the larger question of why so much New Zealand vegetation seems vulnerable to invasion by introduced weeds. One reason is that exotic species arrive here without their full load of pests and parasites that hold them in check in their native lands; native plants, having co-evolved with native pests and parasites over millions of years, do not enjoy this luxury. The other side of this coin is that native species have long associations with animals and birds that assist their pollination and dispersal, and mycorrhizal fungi that assist in mineral uptake, whereas it might be expected that introduced species would be disadvantaged in these respects. However, like the native beeches, most introduced conifers, as well as birch, willows and sycamore, mainly rely on wind for both pollination and dispersal. Insect-pollinated introduced trees in the high country appear to be adequately served by the resident insect fauna, and though native seed-dispersing birds have declined severely in abundance, the ubiquitous blackbirds and thrushes ensure that the fleshy-fruited rowan and wild cherry are vigorously dispersed.

When exotic conifers were first introduced their mineral uptake may have been constrained by a lack of compatible mycorrhizal fungi, but any such inhibition has been overcome, since suitable introduced gill and polypore fungi are now widespread. Many native species are more vulnerable to damage by grazing and browsing animals than plants introduced from regions where such animals have always been part of the natural scene. However, this does not seem to be true of the larger dominant native trees; the severe damage that native beech forests sustained during the middle part of the 20th century resulted from insupportably high deer numbers. As far as spread of wilding pines is concerned, grazing is a two-edged sword. On the one hand, pine seedlings are palatable to livestock, but on the other hand, overgrazing can deplete native grassland, thereby providing spaces for pines to colonise.

The susceptibility of New Zealand vegetation to invasion and replacement by introduced plants is a feature shared with other small, isolated landmasses. A small area provides only a small stage for the evolutionary processes that, on continents, lead to a range of species fully adapted to a wide range of environments. Isolation means that species well adapted to comparable environments in other lands have not been able to reach New Zealand through natural means of dispersal.

The youth of most of our landscape and environments in geological terms, combined with isolation, are doubtless the most decisive factors that give rise to the special features of our flora and fauna. In the Oligocene period, 'only' 30 million years ago, our archipelago became reduced to small, subtropical islands of low relief, and the flora became reduced to plants adapted to such conditions. Relief and climate became more varied during the Miocene, but it was only during the Pliocene, some five million years ago, that change quickened and climates and topography began to resemble those of present day New Zealand. The last 2 million years have seen the uplift of high, rugged mountains, development of extensive alluvial plains and terraces from wide, braided riverbeds, and most of the archipelago under ice-age climates when temperatures were, on average, 3–4°C cooler than at present, and briefly as much as 6°C cooler. These conditions provided huge areas of new habitat, and encouraged spectacular bursts of evolution, from ancestral species that arrived though transoceanic dispersal or that were already present in pre-glacial New Zealand. Among the results are our species-rich genera, such as *Hebe* and *Celmisia*.

However, New Zealand environments did not result in the evolution of hardy and vigorously pioneering trees that exhibit the degree of cold- or drought-hardiness and inbuilt winter dormancy or deciduousness that is characteristic of northern hemisphere temperate and subarctic regions. As well as New Zealand's isolation from genetically pre-adapted tree stocks, it is also probable that trees evolve and adapt more slowly than smaller plants because the generations are longer. A further circumstance is that climates fluctuated widely over comparatively short periods. Had ice-age cold in the east of the South Island alternated only with the comparatively harsh climates of present day Canterbury, there might have been enough continuity for truly hardy native trees to have evolved. However, even in the east of the South Island, there were prolonged mild periods, for instance from 9000 to 5000 years ago, when temperature conditions were as equable as those now prevailing in the milder parts of New Zealand, and native trees adapted to these conditions pre-empted most of the landscape.

Why should we protect the high country from invasion by exotic trees, and how should we do it?

The first part of the question has been answered many times, and we need only to refer to the rules of our own Society, which says that we "promote the preservation of New Zealand plants in their natural habitat". Such views are not universal, however. One 19th century view was that the Lord erred in providing a deficient biota and that is our mission to remedy this, though we would put it rather differently today. The Forest Research Institute, which in the mid 20th century had a mission to combat erosion and depletion of vegetation in the high country, carried out research to find overseas trees that could succeed where native trees appeared to fail. The efforts bore some fruit – many would say too much. Today it is generally accepted that high country erosion is a response to high precipitation and very rapid rates of tectonic uplift, and that what can be lost or gained by de- or re-vegetation is small in proportion. With the rise of the conservation ethic, the attitude has developed that native vegetation should be protected, conserved or restored wherever practicable. While this is admirable, it has to be considered in the light of realities. Among these are that many people, especially those who live in the high country, quite reasonably consider that exotic trees have qualities in respect of amenity, shelter and timber that cannot be fully satisfied by native trees, even given that the qualities of the latter have been underestimated.

Further, there are already virtual forests of wilding conifers, especially around Lake Pukaki and in the Craigieburn Range, which would probably defy destruction by any amount of effort that is likely to be directed towards such an exercise. In practical terms, the best that can be aimed at is to continue and intensify policies and practices that have already been adopted by authorities such as the Department of Conservation and Environment Canterbury. These are to discourage planting of troublesome species; to discourage planting where there is a high risk of spread, e.g. where nor-west gales funnel and carry seed to great distances, or in the case of Douglas fir, close to vulnerable mountain beech forests; and to destroy wildings before they have a chance to bear seed. Ongoing support of this programme depends on public education and support, and this is where members of the Canterbury Botanical Society can make an important contribution.

ACKNOWLEDGEMENTS

I thank Bill Lee, Nick Ledgard and Matt McGlone for comments on earlier drafts of this article.